



Review

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Social niche specialization under constraints: personality, social interactions and environmental heterogeneity

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Several personality traits are mainly expressed in a social context, and others, which are not restricted to a social context, can be affected by the social interactions with conspecifics. In this paper, we focus on the recently proposed hypothesis that social niche specialization (i.e. individuals in a population occupy different social roles) can explain the maintenance of individual differences in personality. We first present ecological and social niche specialization hypotheses. In particular, we show how niche specialization can be quantified and highlight the link between personality differences and social niche specialization. We then review some ecological factors (e.g. competition and environmental heterogeneity) and the social mechanisms (e.g. frequency-dependent, state-dependent and social awareness) that may be associated with the evolution of social niche specialization and personality differences. Finally, we present a conceptual model and methods to quantify the contribution of ecological factors and social mechanisms to the dynamics between personality and social roles. In doing so, we suggest a series of research objectives to help empirical advances in this research area. Throughout this paper, we highlight empirical studies of social niche specialization in mammals, where available.

1. Introduction

Animals are often considered to be able to change their behaviour very quickly in response to changes in their immediate environment and thus to display important behavioural flexibility [1]. Among behavioural traits, social behaviours are seen as the most flexible because the behaviour of one individual depends on a complex dynamic of interactions with its conspecifics. Individuals in a population, however, differ in many aspects of their behaviour such as aggressive tendencies, activity or sociability [2,3]. Despite such behavioural flexibility, individuals in most species nonetheless exhibit consistent differences in their average behavioural phenotypes over time or across situations, a feature generally called personality or temperament differences [4,5]. In addition to behaviour, biologists have also recently reported individual differences in metabolism, endocrinology, immunity, life history and ecology and have found that these features are generally combined together to form syndromes [1,3,5–7]. One main question in evolutionary biology is to understand what constrains the flexibility of behavioural traits (i.e. why not every individual is able to express the most appropriate behaviour in any given situation) and how individual differences are maintained in natural populations despite the assumed standardizing role of natural selection.

Niche specialization can provide an explanation for the maintenance of personality differences: individuals differ in the portion of the whole ecological niche that their population (species) occupies and show niche specialization [3,8–10]. Individual niche specialization is particularly interesting, because it offers a possible explanation for the maintenance of individual differences in a context where natural selection is generally assumed to decrease these differences: the coevolution of habitat-specific performance and habitat preference

can theoretically lead to the evolution of multiple, locally adapted, specialists [8,9,11,12].

This idea of niche specialization has been lately transposed to the social context: individuals may be able to select particular social conditions and avoid others. Populations may thus show social niche variation, and individuals within a population may show social niche specialization [2,13–15], or may occupy different social roles [14]. Social roles, ‘the realised behaviour or tactic an individual uses in response to social challenges such as competing for food, space or mating partners’ [14, p. 504], have been the focus of various studies using an adaptive approach (i.e. optimality or game theory). Social roles have also been assumed to be—and are to a certain extent—flexible [14]. The concept of social niche specialization, however, implies that individuals show consistent differences in their social behaviour and in their ability to select particular social conditions over others, and it is conceivable that personality differences in a social context reflect/affect an individual’s social specialization [2,13–15]. Several personality traits in animals, such as aggressiveness or sociability, are expressed in a social context [7]. Other traits such as boldness, activity or exploration, which can be measured in solitary individuals, can easily be affected by the social context in which an individual is observed [7]. It is therefore natural to link the study of personality to that of social behaviour and organization. However, to date we still do not know the details of the complex dynamics between personality and social niche specialization, and how optimality and game theoretical mechanisms affect this dynamics.

In this paper, we present the hypotheses of ecological and social niche specialization. We then examine the ecological factors that may favour niche specialization and the adaptive mechanisms from optimality and game-theoretic models that explain the evolution and the maintenance of distinct social roles in a population. We highlight how social niche specialization may depend on these mechanisms using empirical studies of social niche specialization in mammals where available. We present a conceptual model and methods to study the dynamics between personality (and other traits) and social roles. Finally, we propose a series of research objectives and approaches that could improve our knowledge on the coevolution of personality and niche specialization and its consequences on the social structure of mammal populations.

2. Ecological factors and social niche specialization

Individual phenotypic differences could arise from individual niche specialization. That is, individuals could express restricted and specific portions of the whole behavioural repertoire of their population (or species) [2], and this portion of the whole behavioural variation may be related to their use of restricted and specific ecological conditions [8–10]. According to ecological niche specialization theory, the niche of a population is the result of the niches occupied by all its individuals [8]. Thus, the variance in the niche of a population (i.e. total niche width, TNW) can be decomposed into a variance component caused by niche differences between individuals (i.e. the between-individual component, BIC) and into a component caused by the width of each individual’s niche (i.e. the within-individual component, WIC). Individual niche specialization occurs when the WIC is low relative to

TNW, the ratio of WIC/TNW, where $TNW = WIC + BIC$, reflecting the extent of ecological niche specialization [8,9]. When individuals’ niches show a complete overlap, this ratio equals 1, and there is no specialization (i.e. individuals are generalists). By contrast, a ratio of 0 indicates no overlap among individuals’ niches. WIC/TNW index has the advantage of being standardized and thus being comparable among species, taxa or populations that differ in ecological conditions. Araujo *et al.* [9] have compared this index among different taxa and found that mammals, with a ratio of 0.3, represented the group with the highest level of diet specialization within populations (average ratio for all the species = 0.66 ± 0.21). Mammals are thus a group where we can expect to find high levels of individual niche specialization.

WIC/TNW expresses the average degree of specialization of individuals in a given population. However, individuals may also vary in their degree of specialization. Hence, within a given population, some individuals with very specific niches (i.e. specialists) strongly contribute to the decrease in WIC/TNW, whereas other individuals with wider niches (i.e. generalists) increase this ratio. Individual indices of specialization such as IS (the mean proportional similarity between an individual’s behavioural repertoire and the population’s repertoire) or \bar{W} (the mean likelihood that an individual’s behavioural distribution matches the population’s distribution for this behaviour) may be used [16], or other indices of variance ratio can be used to quantify the degree of specialization of each individual [2]. Care must be taken with sampling errors when comparing individual indices of specialization [2].

Ecological niche specialization bears some similarity to the concept of personality (see above), and it is tempting to ask whether individual niche specialization is associated with individual behavioural specialization. We expect that, if personality reflects or affects individual niche specialization, the repeatability (r) of a personality trait in a population should be negatively related to WIC/TNW (i.e. populations showing high consistency in a trait may show a high degree of specialization). To date, very few studies have shown a link between personality differences and some aspects of an ecological niche such as diet, habitat use or specialization against predators in mammals [17], and there is no study showing repeatability estimate for both personality and WIC/TNW.

Although ecological niche specialization models have been developed while thinking of features such as habitat or diet choice in animals, they can be easily transposed to social niche specialization [14]. For example, individuals in a population differ in their tendency to disperse or to stay in their natal site; they acquire different dominance ranks; or they opt for different reproductive tactics. In addition to classical indices used in niche specialization studies [16], one could estimate the repeatability of the frequency of each type of social interactions in a population, or could use social network analyses indices (e.g. degree or betweenness) to characterize how individuals in a population differ in their social interactions [18]. Social niche specialization may also be considered as a particular facet of the overall ecological niche specialization if both have coevolved together. For example, some individuals may prefer habitats characterized by a lower density of competitors but also a lower resource abundance. In contrast, social niche specialization may sometimes interfere with ecological niche specialization. For example, an individual may prefer a particular habitat,

but may be rejected from this habitat by competition with conspecifics, as in situations of source-sink dynamics [19].

The literature on ecological niche specialization can provide some information on the ecological factors that facilitate the evolution of social niche specialization [9]. For example, relaxed competition and resource partitioning have been considered to be a consequence of ecological niche specialization [11]. Intraspecific competition is thus a main driver of specialization, but specialization is also facilitated by habitat heterogeneity and ecological opportunity [9]. By contrast, predation and interspecific competition may have various consequences for specialization [9]. Bergmüller & Taborsky [14] have suggested that competition for resources was an important factor leading to social niche specialization through character displacement. We may thus expect the degree of specialization and associated personality differences to increase with the level of intraspecific competition. However, the link between competition and social specialization may be more complex than expected as it probably also depends on the possible alternative outcomes related to each niche. As WIC depends on the diversity of resources available [9], so we can expect social niche specialization to depend on the diversity of social interactions and social situations available to an individual. Furthermore, specialization in the social context displays a characteristic that the ecological context does not: by becoming more socially specialized an individual may generate novel social opportunities for its conspecifics, and thus improve the potential for social niche specialization in its population. Therefore, highly social species may show higher potential for WIC in social niche specialization than lowly social or solitary species. Finally, social niche specialization is probably favoured by trade-offs. For example, we should expect a link between social niche specialization, personality and life-history strategies.

3. Adaptive mechanisms contributing to social roles

Optimality and game-theoretic models have proved very valuable tools for investigating the decision-making processes that lead individuals to adopt particular social roles. They rely on the assumption that individuals should pick a social role that maximizes their net benefits. These models have been extended to acknowledge several constraints on individual decision-making, and it is conceivable that these constraints lead to social niche specialization. Although such mechanisms have rarely been considered from a niche specialization perspective, adaptive models can be used to show the effects of selective forces on the WIC and on the BIC of niche width.

(a) State dependence

Despite potential flexibility, individuals may show consistent differences in behaviour whenever their behaviour is associated with different fitness costs and benefits that depend on a particular state value [20,21]. Individuals could, for example, differ in their boldness because they differ in size [22] or energy reserves [23]. The social role occupied by an individual in a group may exert stable effects on the costs and benefits of expressing a particular behaviour (i.e. act as a state), maintaining consistent behavioural differences

among individuals [14,24]. Furthermore, individuals often behave in a particular way to maintain theirs or others' social roles. This is the case for dominant individuals in cooperative breeding species, where they consistently suppress the reproduction of subordinate animals [25]. An individual's state or social role and their behaviour may thus interact, such that small initial differences in state among individuals may lead to increased differences in both state and behaviour over time [23,26]. These feedback dynamics may have evolved because not all the combinations between a given social role (or state) and particular behavioural features provide the same fitness returns [26]. For example, an individual's fitness benefits depend on both the behavioural patterns it expresses and its experience (state) [27,28].

We can use this state-dependent hypothesis to make some predictions about social niche specialization. First, the feedback dynamics between state and behavioural features should lead to an increase in the BIC or a decrease in the WIC with age. This could be tested by examining if, with age: (i) individual behavioural repertoires decrease their overlap, or (ii) the rate of change in discrete social roles from time to time decreases. Second, most state variables fluctuate over time [29] or differ according to the habitat [30]. Furthermore, some state variables are less flexible than others (e.g. it is simply not possible for an animal to lose half of its body mass in a few minutes). We may therefore expect that within-individual variance in a behavioural trait increases with the within-individual variance in the state itself. Finally, although some researchers have drawn attention to the study of niche specialization consistency over time [14], no study to date has integrated the constraints associated with variation in state into a social niche specialization framework. More details will be given in §5 on how to analyse changes in WIC and BIC of niche width and in TNW.

(b) Frequency dependence

The benefits and costs of a particular behaviour often depend on the behaviour of other group members [31]. In many cases, the fitness payoff associated with a given behaviour decreases with the frequency of individuals expressing this particular behaviour in the population. Such a negative frequency-dependent mechanism may lead to the coexistence of individuals expressing different behaviours or tactics within the population [31]. Increasing niche specialization may also occur through social heterosis, when individuals that show a particular behaviour phenotype benefit from interacting with individuals with dissimilar behavioural phenotypes [32]. In foraging groups, for example, shy individuals may benefit from the presence of bold individuals in risky predatory situations. Interestingly, groups with mixed levels of boldness displayed a higher foraging success than homogeneous groups composed of only bold individuals [33]. Although negative frequency-dependent mechanisms may contribute to social niche specialization, they do not always lead to consistent individual differences in behaviour. For example, individuals could specialize in a different social role or behaviour at each time unit, thus maintaining BIC but without leading to any consistency in such differences [8,34]. By contrast, among socially foraging sheep, bold individuals contribute consistently more to group fission events [35]. Negative frequency dependence may also maintain a higher TNW by forcing individuals to

adopt different social roles. Through its effect on TNW, such mechanisms may thus affect the extent of social niche specialization in unpredictable ways, with the outcome depending mainly on the effects of such mechanisms on the BIC relative to their effects on TNW. Conversely, positive frequency dependence may also occur when individuals match their behaviour with those of other group-mates through consensus decision-making [36] or in an effort to be less conspicuous (i.e. 'conformity', [37]). In that case, positive frequency dependence would constrain TNW and thus the expression of social niche specialization.

(c) Social awareness and eavesdropping

Another, often overlooked, explanation for consistent individual differences in behaviour is to consider situations where it is profitable for an individual to be predictable [21]. For example, in a resource-defence context, it may be beneficial for aggressive individuals to be recognized as such [38], as this may reduce the probability of escalated fights with conspecifics and/or facilitate mate choice [21,39]. Interestingly, the presence of a small number of socially aware individuals, that adjust their behaviour to the behaviour of their partners, can select for consistent individual differences in the tendency to cooperate or defect [40]. Similarly, Wolf *et al.* [41] showed that the same mechanism might lead to different levels of aggressiveness and plasticity during dyadic contests within populations. Such mechanisms would lead to a decrease in the niche's WIC, and in some cases stabilize the BIC. Such models are particularly likely to apply to social species, where individuals often maintain stable groups, develop long-term bonds and interact repeatedly with each other. Empirical tests of such models remain scarce and none have been attempted with mammals yet.

4. Decision-making under constraints: including individual variation and environmental heterogeneity in optimality models

(a) Individual variation

Models of frequency dependence typically assume that all individuals are equivalent and interchangeable. However, negative frequency dependence, consensus decision-making, conformity and social heterosis may affect individuals differently as a function of their phenotype. For example, shy perch (*Perca fluviatilis*) adjust their behaviour to the behaviour of other shoal mates more than bold ones [42]. Similarly, shy guppies (*Poecilia reticulata*) benefit to a greater extent from the presence of conspecifics than bold guppies, and become bolder in the presence of conspecifics [33]. Shy individuals may also adjust their behaviour more with social context because they are better able to use public or social information [43]. This interesting and surprisingly ignored feature of frequency-dependent mechanisms may greatly affect how and to what extent individuals specialize in different social niches, as well as the evolution of behavioural differentiation. If frequency-dependent mechanisms affect individuals differently, we may expect WIC and BICs, and TNW to respond differently to such mechanisms based on the phenotypic composition of the group. Another overlooked implication of such individual differences is that

populations may display individual variation in their WIC, potentially leading to mixes of individuals with different levels of behavioural consistency or different levels of social niche specialization [2]. The presence of generalists in populations greatly affects the predicted dynamics of behavioural differentiation through evolution. Clearly, more studies are needed to investigate precisely the nature of frequency-dependent mechanisms affecting the behaviours of different types of individuals in mammal species.

Most models of social dynamics also assume that all individuals have roughly the same impact on the overall social conditions. It may, however, not be systematic. A limited number of 'keystone' individuals have a crucial role for information transmission, labour management or conflict policing [44]. In primates, such keystone individuals have been implicated in conflict policing [45,46], and this warrants further study. Dominants or leaders may also have disproportionate effects on group structure [47], and it has been suggested that such individuals may promote individual differences by enabling conspecifics to occupy different alternative social niches. Hence, the occurrence of such keystone individuals would increase the extent of BIC in social groups.

(b) Environmental heterogeneity

Game theoretical models typically assume that individuals interact in a random fashion within populations, independent of other individual features [31]. Interactions among group members, however, may be affected by consistent behavioural differences. For example, guppies that are bolder towards a potential predator entertain fewer and weaker interactions with shoal mates [48]. Individuals may also use different habitats depending on their boldness [49,50], which may limit their interactions with individuals having a different personality [51,52]. Non-random interaction patterns may greatly affect the outcome of game theoretical models [24,53,54]. Non-random interactions are an especially ubiquitous form of environmental heterogeneity, leading individuals to experience a 'patchy' social environment. Acknowledging such variation greatly affects the predicted frequency-dependent dynamics [55], and social network metrics may provide powerful tools to study the relationship between personality distribution in a group, its structure and interaction patterns among group members [24,56].

Variation in the social environment also needs to be accounted for because individuals may express their differences only in the presence of conspecifics, a phenomenon termed social facilitation. For example, individual perches (a social species) fail to express differences in boldness to predation risk when tested alone, but differ when tested in shoals [57]. Taking the social environment and the behaviour of other group members into consideration is also necessary to detect behavioural syndromes. For example, both the behaviour of shoal mates and the social context need to be accounted for in order to detect a relationship between boldness and exploration in Eurasian perch [57]. Social facilitation, competition and ontogenetic processes, such as habituation and previous experience, may also generate and maintain consistent differences in personality even in the absence of initial differences among individuals [58,59]. Interestingly, social facilitation, competition and ontogenetic processes are likely to vary in space and time, for example, as a function of the phenotypic composition of the group or of resource abundance. This spatial and temporal

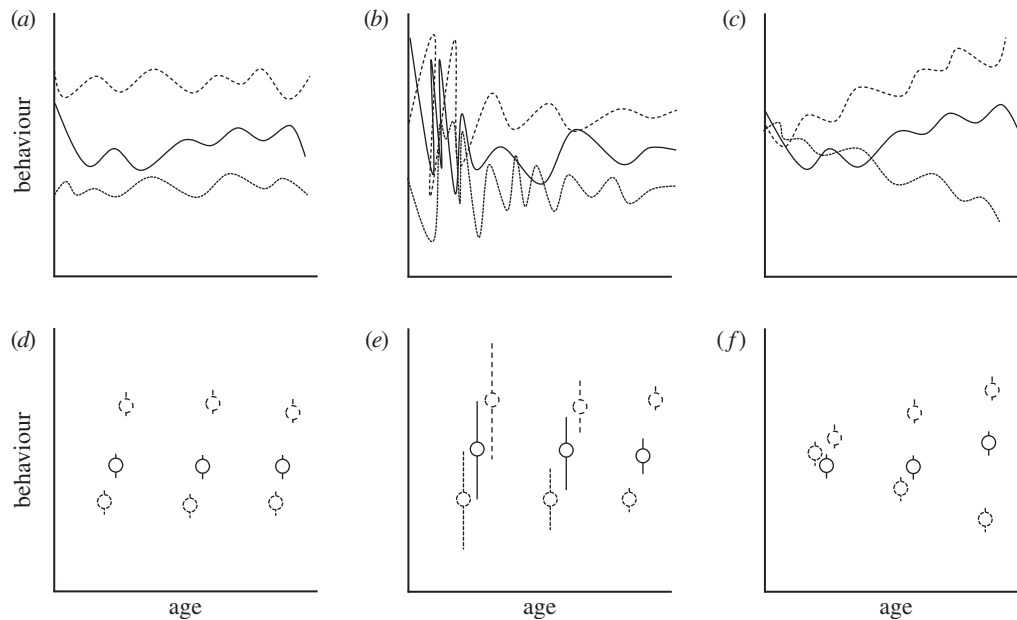


Figure 1. Testing the hypothesis of the ontogeny of individual social specializations. (a–c) The hypothetical developmental trajectories of a behaviour trait for three different individuals (or genotypes). (d–f) The average values and the phenotypic variances for the trait measured for the three individuals at three different ontogenetic stages. In the first case (a,d), we can see that social specialization corresponds to a decrease in within-individual variance of the trait with age and a relatively stable between-individual variance and average value; individuals are getting specialized through ontogeny by reducing their plasticity with age. In the second case (b,e), the between-individual variance is getting relatively larger than the within-individual variance with age, and thus individuals are getting specialized as they grow older. In the third case (c,f), the ontogeny of specialization results from an increase in the between-individual variance relative to the within-individual variance; individuals change their phenotype with age and show different developmental reaction norms.

variation leads to increased environmental heterogeneity and may generate local constraints on TNW, the BIC and the WIC. We think that much could be gained by integrating these additional mechanisms into current models with frequency- or state-dependent mechanisms. In particular, little is known on how group composition, size and environmental pressures, such as predation risk, affect conformity [15], and studies of frequency-dependent mechanisms under varying group conditions will surely provide fruitful results and insights on behaviour through social niche specialization [14,24].

Finally, individuals may display social niche construction. That is, they could impact or manipulate the behaviours of their conspecifics in a way that creates a favourable social environment for their phenotype (for example, their particular level of boldness or aggressiveness). Social niche construction would lead to increased consistency of social roles and to niche specialization by stabilizing the BIC [10]. Niche construction could also increase TNW, by allowing some individuals to express certain types of behaviours that would not be favoured in the absence of niche construction. Interestingly, keystone individuals, through their higher influence on the social environment, may have a higher potential for social niche construction, thereby contributing to the maintenance of consistent behavioural differences among group members [46]. This aspect of animal personality is acknowledged [55], although it has rarely been investigated empirically.

5. How to study social niche specialization

(a) Social niche specialization as a behavioural reaction norm: three possible scenarios

An individual's social role and personality at any stage of its life can be thought of as the result of a dynamic series of

interactions between inherited genetic (i.e. additive or dominance genetic) effects, epigenetic (e.g. parental effects, early environment effects) background, and the particular social environment that the individual has encountered [10]. For example, mother–offspring interactions permanently affect anxiety, exploration and social behaviour in rodents [60,61] and primates [62]. Likewise, sibling interactions early in life may affect personality as an adult [63]. As a result, a behavioural reaction norm approach [64], where the social role of individuals in a population is studied as a function of their personality, the interaction between individuals/genotypes and different social conditions, is a powerful way to investigate social niche specialization.

In §3a, we mentioned the possibility for state dependence to generate social niche specialization with age. It is possible to use a behavioural reaction norm approach [10,64] to analyse the combined effects of the genetic background (or other early sources of individual differences) and the social environment on the development of social role or personality differences. Social niche specialization may arise through three distinctive developmental scenarios (figure 1): (i) absence of feedback mechanism between individuals and their social environment (figure 1a), such that individual social roles/personality are mainly influenced by genetic or permanent developmental effects (e.g. maternal effects); hence, WIC, BIC or repeatability should be constant throughout life (figure 1d); (ii) developmental constraints on flexibility (figure 1b), where the social roles taken by individuals overlap early in life but become increasingly distinct over time (developmental niche specialization); we thus expect within-individual variance to decrease with age, but between-individual variance to stay constant, and therefore the repeatability of the trait to increase over time (figure 1e); (iii) constraints on individual developmental trajectories (figure 1c), where BIC

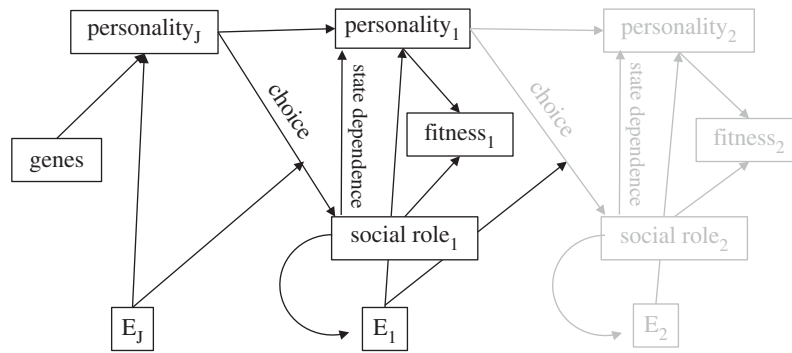


Figure 2. Graphical representation of the hypothetical links between personality and social roles that can lead to social niche specialization. An individual's personality (i.e. personality_J; P_J) at a juvenile stage depends on the genes inherited from the parents and responds to early (E_J) environmental conditions (covariance and interaction between gene and environment are not shown here). In the particular social context of the paper, E_J consists of various social conditions affecting the individuals (e.g. parental effects, conflicts among siblings, population density or competition), but we can easily extend them to non-social conditions such as food abundance or risks of predation. Because of genetic and experiential effects P_J may affect both personality at the next time step (P_1) and the choice of a particular social role (i.e. social role₁; SR_1). This choice may also depend on the environmental conditions encountered by the individual prior to period 1. For example, frequency-dependent selection or specific social contexts (e.g. age structure, population density, sex ratio, competition and social interactions with conspecifics) may alter the choice of a social role based on personality. The specific social role chosen by the individual may in turn affect personality expression. Combinations between personality and social role may translate into different fitness outcomes (i.e. fitness₁; W_1). For example, territorial individuals may perform better when they are bold or aggressive than when they are shy or lowly aggressive. By contrast, floaters may do better by being thorough explorers. By choosing a particular social role, an individual may affect the environmental conditions (E_1), because it changes the proportion of individuals with a given social role. Environmental conditions can in turn modify the personality of the individual and alter its choice of a social role at the next time step (SR_2). Finally, social conditions generated by the choice of social roles or personality of conspecifics can interfere on the link between an individual's personality and fitness. The same pattern can be repeated over time (represented in grey in the figure).

and repeatability should increase over time (i.e. individual slopes differ among individuals), while WIC remains constant.

Constraints on flexibility may be caused by two main mechanisms. (i) Reversible plasticity is assumed to evolve in response to temporal or spatial environmental heterogeneity occurring within the lifetime of an individual [65]. Within-individual variance reflects the ability of an individual to change its phenotype in a reversible way in response to environmental changes, and thus large WIC early in life should reflect a high heterogeneity in environmental conditions experienced by young individuals. Phenotypic plasticity at a young age, therefore, may be selected to allow an individual to adjust its phenotype to the diversity of environmental conditions it may encounter. Then aging individuals may specialize through niche selection and niche construction ([10]; see §4b), thereby reducing environmental variation on the phenotypic expression of their traits. (ii) Alternatively, strong selection against flexibility, with only the most stable individuals surviving to reach old age could explain a decrease in WIC with age. To avoid this issue, care has to be taken to conduct longitudinal studies of individuals. With the constraint on individual trajectory hypothesis, we may expect strong stabilizing selection on personality/social role, leading to canalization of the trait early in life but a relaxation at later ages [66]. Maternal effects may counteract the additive genetics effects and reduce BIC early in life, but may decrease in importance to reveal genetic differences at a later age [66].

We can model behavioural reaction norms using mixed models, analysing the social role expressed by individuals as a function of their pedigree, development and personality (table 1a). We can test the constraint on flexibility hypothesis (figure 1b,e) by estimating BIC and WIC as a function of age using a random regression with heterogeneous residuals [68]. The technical statistical details behind mixed models can be found elsewhere [64,67]. A recent review on repeatability in

behaviour traits [69] has not confirmed the general hypothesis that repeatability increases with age. The scarcity of published results, however, does not allow us to make any strong inference development of social niche specialization and personality in mammals and other taxa.

(b) Feedback dynamics between personality and social role

Initial differences in personality may determine the social role taken by individuals, but the social role itself may further affect the expression of personality differences among individuals over time. In order to analyse the interaction between personality and social role, studies must use longitudinal data, following both personality (figure 2; 'personality_J', 'P₁', 'P₂', etc.) and social roles ('social role₁', 'SR₂') over more than one time step. In particular, personality has to be measured prior to social role to determine how personality affects social role ($P_J \rightarrow SR_1$), and to see how social role affects personality ($SR_1 \rightarrow P_1$) independently of the consistency of personality ($P_J \rightarrow P_1$). Longitudinal data on personality and social roles also enable us to tease apart the mechanisms contributing to feedback between personality differences and social roles. For example, by combining longitudinal data on social role and personality with an estimation of the fitness, we can study the contribution of social awareness and experience to social niche specialization. Social awareness should be associated with a constant relationship between the social role expressed by an individual and its fitness, irrespective of the time spent expressing this particular social role ($SR_1 \rightarrow W_1 = SR_2 \rightarrow W_2 = SR_3 \rightarrow W_3$). Moreover, since social awareness favours consistency in a similar way for all individuals throughout their lifespan, we may predict that the likelihood for an individual of expressing a different social role over time will be constant (i.e. $SR_1 \rightarrow SR_2 = SR_2 \rightarrow SR_3$). By contrast, if individuals specialize in a social role because they

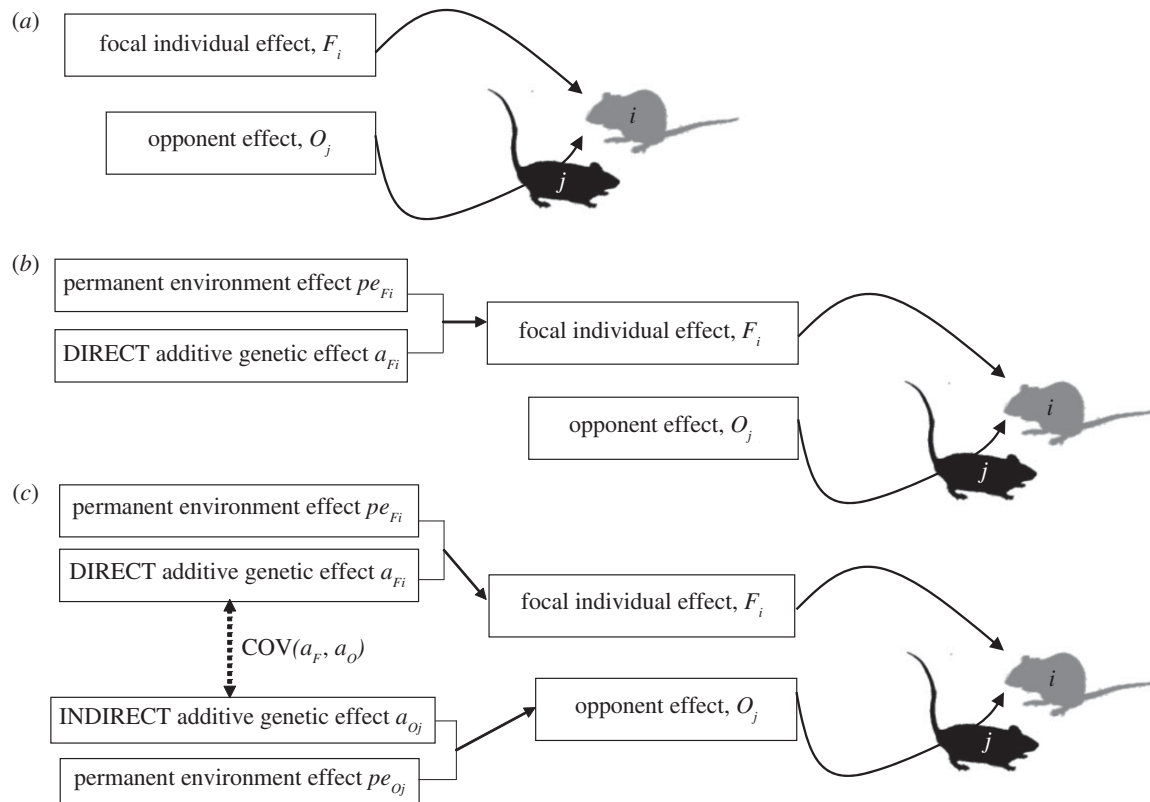


Figure 3. Direct and indirect effects on aggressive behaviour in deer mice (adapted from Brommer *et al.* [75]). Several models are generated to decompose the components of total phenotypic variance in the aggressive trait measured in the focal individual. (a) Both individual i (i.e. direct) and opponent j (i.e. indirect) effects are fitted. (b) Pedigree information allows the researcher to decompose the direct individual effects into permanent and additive genetic effects. (c) Pedigree information makes it also possible to decompose the opponent effects into indirect, permanent and additive genetic effects, and to estimate the correlation between direct and indirect genetic effects.

Table 1. General mixed models used to quantify and investigate social niche specialization in animal populations. Mixed models may included fixed (normal), random (i.e. random intercepts, bold) effects and interactions between these two (i.e. random slopes). We detail three general forms of models especially useful for quantifying the contribution of all the mechanisms we outline in this review, along with the variance components they estimate (*sensu* Dingemanse & Dochterman [67]). We also summarize the data necessary to use the models. For additional details and the technical aspects of model fitting, see [67]). SR, individual social role; T, time or age of individuals; ID, individual identity; ENV, social environment variable (interactant identity or social group); P, personality measure; W, individual fitness measure; V_{ind0sr} , individual variance in social role (intercept of the reaction norm); V_{ind1sr} , individual variance in social role plasticity (slope of the reaction norm); V_{int0sr} , individual variance in indirect effect; V_{ind0w} , individual variance in fitness (intercept); $COV_{ind0sr, ind0p}$, covariance between mean social role and personality (among individuals); $COV_{e0sr, e0p}$, covariance between changes in social role and personality (within individuals); URSM, Univariate Random Slope model; URIM, Univariate Random Intercept model; MRIM, Multivariate Random Intercept model).

model	formula	variance components estimated	data
A behavioural reaction norm (URSM)	$SR \sim T + ID + T \times ID$	V_{ind0sr} V_{ind1sr}	repeated observations of social role for each individual at different ages
B indirect (genetic) effects (URIM)	$SR \sim ID + ENV$	V_{ind0sr} V_{int0sr}	repeated observations of social role in social settings (each individual tested repeatedly as a focal and as an interactant).
C personality-dependent performance (URIM)	$W \sim SR + P + P:$ $SR + ID$	V_{ind0w}	repeated fitness measurements
niche-picking (MRSM)	$(SR; P) \sim ID$	$COV_{ind0sr, ind0p}$ or $COV_{e0sr, e0p}$	repeated measurements of personality and social role.

increase their performance through learning, fitness should increase with the time spent expressing the same social role ($W_2 > W_1$, if the individual expresses the same social role). In the same way, we predict an interaction between SR_1 and P_1

on the choice of SR_2 . Likewise, SNS through learning and experience predicts a decreasing likelihood of changing social role as the animal get more experienced in a given social role ($SR_2 \rightarrow SR_3 > SR_1 \rightarrow SR_2$).

(c) Constraints on social roles

Sections 3 and 4 examined how the social role of an individual depends on the behaviour and social role of conspecifics and consequently their genotype. Such effects are often termed indirect (genetic) effects (IGE) [70,71] and may be integrated within a behavioural reaction norm approach to quantify how they contribute to social niche specialization. Including IGE within our framework renders possible the study of developmental effects associated with maternal environment, and the effects of the social interactions on the social role expressed by individuals [66,71–74]. To estimate IGE on an individual's social role, we need to measure the individual's traits successively in the presence of different conspecifics (or interactants) of known identity (table 1b). This design, coupled with pedigree information, permits an estimate to be made of both direct and indirect genetic effects (figure 3). For example, in Wilson *et al.*'s [72] study on aggressiveness, each deer mouse (*Peromyscus maniculatus*) encountered several same-sex individuals in a neutral arena, either as a focal animal or as an opponent. It was found that individuals differed in their intrinsic aggressiveness, but also that they differed in their ability to trigger aggressive reactions from the focal individual. This approach would also be extremely powerful to investigate the impact of keystone individuals on the overall social environment. We are not aware of any study that attempted this. Keystone individuals could impact the environment by affecting the social roles available to individuals over their lives (i.e. WIC). For example, Sih & Watters [76] documented a situation in water striders (*Aquarius remigis*) where a few males, by being extremely aggressive, had a disproportionate effect on the overall mating dynamics (see §4). In this case, one could quantify precisely the impact of hyper-aggressive males by analysing the effect the presence of such males has on the social role expressed by each individual. Similarly, the relationship between the social environment, personality, social role and its fitness consequences will allow us to investigate social niche construction. Gathering this type of data over different habitats, or differing social systems, or according to the frequency of certain social roles may greatly advance our understanding of social niche specialization and personality differences. Alternatively, Lea *et al.* [18] studied the quantitative genetics of individuals' social network indices (i.e. out-degree, in-degree, attractiveness, expansiveness, embeddedness and betweenness) in a yellow-bellied marmot (*Marmota flaviventris*) population. They found a strong effect of the social group and, to a lower extent, additive genetic (i.e. direct) effects on both affiliative and agonistic behaviour.

(d) Social niche specialization through personality-dependent social preferences and performance

Social niche specialization may arise from the fact that an individual with a given personality does not perform well in every social situation (i.e. personality-dependent performance). It may, therefore, be possible that individuals select some particular social roles and avoid others (a phenomenon referred to as niche-picking; [10]). The maintenance of social niche specialists through evolution may be the result of the coevolution between personality-dependent performance and niche-picking. With a behavioural reaction norm approach, it is possible to assess how personality-dependent social

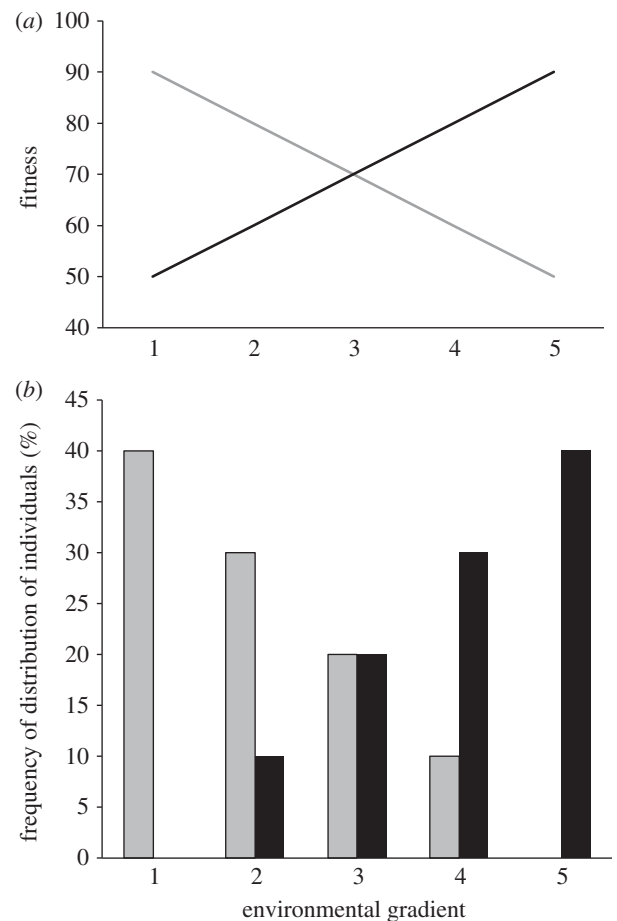


Figure 4. The link between habitat-specific performance and habitat preference. (a) Hypothetical fitness function of two different personality types (e.g. extreme shyness and extreme boldness) in an environmental gradient (habitat-specific performance). (b) Distribution of the two personality phenotypes as a function of the environmental gradient (habitat preference).

performance and niche-picking coevolve to maintain personality differences. This is achieved by, first, investigating how the fitness of individuals in a given social role varies as a function of their personality (figure 4a and table 1c). This has been shown in the case of general environmental condition and in the case of social conditions. In pulse resource systems, different personality types can perform differently depending on food availability [63,77], but, surprisingly, we are not aware of any study with similar results on personality and social roles. Second, we need to investigate whether animals with different personalities show preferences for particular social roles, potentially depending on the overall environmental conditions (figure 4b and table 1c). For instance, juvenile green lizards' dispersal decisions depend on the interaction between their sociability and population density in their natal habitat [78]. In the western mosquitofish (*Gambusia affinis*), individuals with different levels of sociability choose different types of shoals and shoal size [79]. In *Drosophila melanogaster*, males distribute in a non-random way depending on their level of aggressiveness, and fitness is higher when males are housed under the environmental conditions each type preferred [80]. Finally, we would have to show the presence of a correlation between niche-picking and personality-dependent performance (i.e. a personality by social role correlation) in natural populations.

Individuals could also differ in their degree or capacity for niche-picking (i.e. some may be generalists). If social context choice depends on dispersal ability, then personalities

could vary in their capacity to choose the best social context. There may be a trade-off between an individual's ability to choose a social situation and its level of specialization [14]. These scenarios can be tested either by using data from natural populations or by designing reciprocal transfer experiments. Of course, the hypothetical situation presented in figure 4 is probably not as clear-cut in nature; individuals can make errors in the habitats they choose or may be restricted in their choice by the limited availability of conditions in which they fit best. Dispersal and environmental unpredictability are assumed to constrain the evolution of specialization [12]. Finally, the coexistence of specialized individuals within populations may generate associations among different types of traits in a behavioural [1] or pace-of-life syndrome [7], and it may be important to consider behavioural, life-history and metabolic aspects of habitat or social choice. For example, bold, aggressive individuals, if short-lived and with high metabolic needs [10,33], may perform better in a rich environment where competition and predation rate are high. In contrast, a poor habitat, with low population density and low competition, may favour shy, non-aggressive and long-lived individuals.

6. Conclusion

The point of this paper was to highlight the advantages of incorporating the study of personality into a general ecological and social niche specialization framework. Several interesting hypotheses from these fields can be made that would be certainly fruitful for behavioural ecologists: First,

we show that predictions about ecological factors at the origin of ecological niche specialization can be applied to the study of personality and social specialization. We also show that studying personality or social roles would gain by using a more integrative approach combining heterogeneity and the coevolution between individual habitat preference and habitat-specific performance, frequency or state dependence and social awareness. We also review the importance of considering direct and indirect genetic effects, developmental aspects and the dynamics of feedback effects between personality, social role and the social environment. Despite the strong potential for mammal studies to contribute to the development of future research on these topics, empirical evidence on mammals is still rare. Existing studies dealing with social specialization and personality were strongly biased towards fish, insects and birds. It may be that these taxa are easier to manipulate experimentally. However, the methods necessary for studying the links between personality and social roles are already available and can be easily applied to several long-term, individual-based studies of wild mammals.

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References

- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004 Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241–277. (doi:10.1086/422893)
- Réale D, Dingemanse N. 2010 Personality and individual social specialisation. In *Social behaviour: genes, ecology and evolution* (eds T Székely, AJ Moore, J Komdeur), pp. 417–441. Cambridge, UK: Cambridge University Press.
- Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. 2012 An evolutionary ecology of individual differences. *Ecol. Lett.* **15**, 1189–1198. (doi:10.1111/j.1461-0248.2012.01846.x)
- Gosling SD. 2001 From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86. (doi:10.1037/0033-2909.127.1.45)
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)
- Biro P, Stamps J. 2008 Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* **23**, 361–368. (doi:10.1016/j.tree.2008.04.003)
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc. B* **365**, 4051–4063. (doi:10.1098/rstb.2010.0208)
- Bolnick D, Svanbäck R, Fordyce J, Yang L, Davis J, Husley C, Forister M. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28. (doi:10.1086/343878)
- Araújo M, Bolnick D, Layman C. 2011 The ecological causes of individual specialisation. *Ecol. Lett.* **14**, 948–958. (doi:10.1111/j.1461-0248.2011.01662.x)
- Stamps J, Groothuis TGG. 2010 The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* **85**, 301–325. (doi:10.1111/j.1469-185X.2009.00103.x)
- Ravigné V, Dieckmann U, Olivier I. 2009 Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* **174**, 141–169. (doi:10.1086/605369)
- Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME. 2012 A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* **14**, 841–851. (doi:10.1111/j.1461-0248.2011.01645.x)
- Barash DP. 1997 In search of behavioral individuality. *Hum. Nat.* **8**, 153–169. (doi:10.1007/s12110-997-1009-3)
- Bergmüller R, Taborsky M. 2010 Animal personality due to social niche specialisation. *Trends Ecol. Evol.* **25**, 504–511. (doi:10.1016/j.tree.2010.06.012)
- Webster MM, Ward AJW. 2011 Personality and social context. *Biol. Rev.* **86**, 759–773. (doi:10.1111/j.1469-185X.2010.00169.x)
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. 2002 Measuring individual-level resource specialisation. *Ecology* **83**, 2936–2941. (doi:10.1890/0012-9658(2002)083[2936:MLRS]2.0.CO;2)
- Martin JGA, Réale D. 2008 Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behav. Proc.* **77**, 66–72. (doi:10.1016/j.beproc.2007.06.004)
- Lea AJ, Blumstein DT, Wey TW, Martin JG. 2010 Heritable victimization and the benefits of agonistic relationships. *Proc. Natl Acad. Sci. USA* **107**, 21 587–21 592. (doi:10.1073/pnas.1009882107)
- Pulliam HR. 1988 Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661. (doi:10.1086/284880)
- Houston AI, McNamara JM. 1999 *Models of adaptive behavior: an approach based on state*. Cambridge, UK: Cambridge University Press.
- Dall SRX, Houston AI, McNamara JM. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective.

- Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)
22. McElreath R, Strimling P. 2006 How noisy information can make 'personality' an adaptation: a simple model. *Anim. Behav.* **72**, 1135–1139. (doi:10.1016/j.anbehav.2006.04.001)
 23. Rands SA, Cowlishaw G, Pettifor RA, Rowcliff JM, Johnstone RA. 2003 Spontaneous emergence of leaders and followers in foraging pairs. *Nature* **423**, 432–434. (doi:10.1038/nature01630)
 24. Krause J, James R, Croft DP. 2010 Personality in the context of social networks. *Phil. Trans. R. Soc. B* **365**, 4099–4106. (doi:10.1098/rstb.2010.0216)
 25. Sapolski RM. 1994 Individual-differences and the stress response. *Semin. Neurosci.* **6**, 261–269. (doi:10.1006/smns.1994.1033)
 26. Luttbegg B, Sih A. 2010 Risk, resources and state-dependent adaptive behavioural syndromes. *Phil. Trans. R. Soc. B* **365**, 3977–3990. (doi:10.1098/rstb.2010.0207)
 27. Brown C, Laland K. 2003 Social learning in fishes: a review. *Fish and Fisheries* **4**, 280–288. (doi:10.1046/j.1467-2979.2003.00122.x)
 28. Wolf M, van Doorn GS, Weissing FJ. 2008 Evolutionary emergence of responsive and unresponsive personalities. *Proc. Natl Acad. Sci. USA* **105**, 15 825–15 830. (doi:10.1073/pnas.0805473105)
 29. Dingemanse NJ, Wolf M. 2010 Recent models for adaptive personality differences: a review. *Phil. Trans. R. Soc. B* **365**, 3947–3958. (doi:10.1098/rstb.2010.0221)
 30. Blondel J. 2007 Coping with habitat heterogeneity: the study of Mediterranean blue tits. *J. Ornithol.* **148**, S3–S15. (DOI:10.1007/s10336-007-0161-1).
 31. Maynard-Smith J. 1982 *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
 32. Nonacs P, Kapheim KM. 2007 Social heterosis and the maintenance of genetic diversity. *J. Evol. Biol.* **20**, 2253–2265. (doi:10.1111/j.1420-9101.2007.01418.x)
 33. Dyer JRG, Croft DP, Morrell LJ, Krause J. 2009 Shoal composition determines foraging success in the guppy. *Behav. Ecol.* **20**, 165–171. (doi:10.1093/beheco/arn129)
 34. Dubois F, Giraldeau L-A, Réale D. 2012 Frequency-dependent payoffs and sequential decision-making favour consistent tactic use. *Proc. R. Soc. B* **279**, 1977–1985. (doi:10.1098/rspb.2011.2342)
 35. Michelen P, Sibbald AM, Erhard HW, McLeod JE. 2008 Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behav. Ecol.* **20**, 145–152. (doi:10.1093/beheco/arn126).
 36. Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW. 2008 Consensus decision making by fish. *Curr. Biol.* **18**, 1773–1777. (doi:10.1016/j.cub.2008.09.064)
 37. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
 38. Botero CA, Pen I, Komdeur J, Weissing FJ. 2010 The evolution of individual variation in communication strategies. *Evolution* **64**, 3123–3133. (doi:10.1111/j.1558-5646.2010.01065.x)
 39. Schuett W, Godin J-GJ, Dall SRX. 2011 Do female zebra finches, *Taeniopygia guttata*, choose their mates based on their "personality"? *Ethology* **117**, 908–917. (doi:10.1111/j.1439-0310.2011.01945.x)
 40. McNamara JM, Stephens PA, Dall SRX, Houston AI. 2009 Evolution of trust and trustworthiness: social awareness favours personality differences. *Proc. R. Soc. B* **276**, 605–613. (doi:10.1098/rspb.2008.1182)
 41. Wolf M, Van Doorn GS, Weissing FJ. 2011 On the coevolution of social responsiveness and behavioural consistency. *Proc. R. Soc. B* **278**, 440–448. (doi:10.1098/rspb.2010.1051)
 42. Magnhagen C, Staffan F. 2005 Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behav. Ecol. Sociobiol.* **57**, 295–303. (doi:10.1007/s00265-004-0834-1)
 43. Marchetti C, Drent PJ. 2000 Individual differences in the use of social information in foraging by captive great tits. *Anim. Behav.* **60**, 131–140. (doi:10.1006/anbe.2000.1443)
 44. Fewell JH. 2003 Social insect networks. *Science* **301**, 1867–1870. (doi:10.1126/science.1088945)
 45. Flack JC, Krakauer DC, de Wall FBM. 2005 Robustness mechanisms in primate societies: a perturbation study. *Proc. R. Soc. B* **272**, 1091–1099. (doi:10.1098/rspb.2004.3019)
 46. Flack JC, Girvan M, de Waal FBM, Krakauer DC. 2006 Policing stabilizes construction of social niches in primates. *Nature* **439**, 426–429. (doi:10.1038/nature04326)
 47. Leblond C, Reeb S. 2006 Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour* **143**, 1263–1280. (doi:10.1163/156853906778691603)
 48. Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J. 2005 Assortative interactions and social networks in fish. *Oecologia* **143**, 211–219. (doi:10.1007/s00442-004-1796-8)
 49. Wilson DS, Coleman K, Clark AB, Biederman L. 1993 Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J. Comp. Psychol.* **107**, 250–260. (doi:10.1037/0735-7036.107.3.250)
 50. Wilson DS. 1998 Adaptive individual differences within single populations. *Phil. Trans. R. Soc. Lond. B* **353**, 199–205. (doi:10.1098/rstb.1998.0202)
 51. Schürch R, Heg D. 2010 Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behav. Ecol.* **21**, 588–598. (doi:10.1093/beheco/arn024)
 52. Michelen P, Jeanson R, Deneubourg J-L, Sibbald AM. 2010 Personality and collective decision-making in foraging herbivores. *Proc. R. Soc. B* **277**, 1093–1099. (doi:10.1098/rspb.2009.1926)
 53. Croft DP, James R, Krause J. 2008 *Exploring animal social networks*. Princeton, NJ: Princeton University Press.
 54. Nowak MA, May R. 1992 Evolutionary games and spatial chaos. *Nature* **359**, 826–829. (doi:10.1038/359826a0)
 55. Sih A, Hanser SF, McHugh K. 2009 Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* **63**, 975–988. (doi:10.1007/s00265-009-0725-6)
 56. Wey T, Blumstein DT, Weiwei S, Jordán F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344. (doi:10.1016/j.anbehav.2007.06.020)
 57. Magnhagen C. 2006 Social influence on the correlation between behaviours in young-of-the-year perch. *Behav. Ecol. Sociobiol.* **61**, 525–531. (doi:10.1007/s00265-006-0280-3)
 58. Oosten JE, Magnhagen C, Hemelrijk CK. 2010 Boldness by habituation and social interactions: a model. *Behav. Ecol. Sociobiol.* **64**, 793–802. (doi:10.1007/s00265-009-0896-1)
 59. Hellström G, Magnhagen C. 2011 The influence of experience on risk taking: results from a common-garden experiment on populations of Eurasian perch. *Behav. Ecol. Sociobiol.* **65**, 1917–1926. (doi:10.1007/s00265-011-1201-7)
 60. Kaiser S, Kruijver FPM, Swaab DF, Sachser N. 2003 Early social stress in female guinea pigs induces a masculinization of adult behavior and corresponding changes in brain and neuroendocrine function. *Behav. Brain Res.* **144**, 199–210. (doi:10.1016/S0166-4328(03)00077-9)
 61. Meaney M. 2001 Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annu. Rev. Neurosci.* **24**, 1161–1192. (doi:10.1146/annurev.neuro.24.1.1161)
 62. Coplan JD, Andrews MW, Rosenblum LA, Owens MJ, Friedman S, Gorman JM, Nemeroff CB. 1996 Persistent elevations of cerebrospinal fluid concentrations of corticotropin-releasing factor in adult nonhuman primates exposed to early-life stressors: implications for the pathophysiology of mood and anxiety disorders. *Proc. Natl Acad. Sci. USA* **93**, 1619–1623. (doi:10.1073/pnas.93.4.1619)
 63. Boon AK, Réale D, Boutin S. 2007 The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol. Lett.* **10**, 1094–1104. (doi:10.1111/j.1461-0248.2007.01106.x)
 64. Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010 Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* **25**, 81–89. (doi:10.1016/j.tree.2009.07.013)
 65. Moran NA. 1992 The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139**, 971–989. (doi:10.1086/285369)
 66. Wilson AJ, Réale D. 2006 Ontogeny of additive and maternal genetic effects: lessons from domestic mammals. *Am. Nat.* **167**, E23–E38. (doi:10.1086/498138)
 67. Dingemanse NJ, Dochtermann NA. 2012 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* (doi:10.1111/1365-2656.12013)
 68. Brommer JE, Rattiste K, Wilson AJ. 2008 Exploring plasticity in the wild: laying date–temperature reaction norms in the common gull *Larus canus*.

- Proc. R. Soc. B* **275**, 687–693. (doi:10.1098/rspb.2007.095)
69. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)
 70. Moore AJ, Brodie ED, Wolf JB. 1997 Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* **51**, 1352–1362. (doi:10.2307/2411187)
 71. Bijma P. 2012 A general definition of the heritable variation that determines the potential of a population to respond to selection. *Genetics* **189**, 1347–1359. (doi:10.1534/genetics.111.130617)
 72. Wilson AJ, Gelin U, Perron M, Réale D. 2009 Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proc. R. Soc. B* **276**, 533–541. (doi:10.1098/rspb.2008.1193)
 73. Wilson AJ, de Boer M, Arnott G, Grimmer A. 2011 Integrating personality research and animal contest theory: aggressiveness in the green swordtail *Xiphophorus helleri*. *PLoS ONE* **6**, e28024. (doi:10.1371/journal.pone.0028024)
 74. Wilson AJ, Morrissey MB, Adams MJ, Walling CA, Guinness FE, Pemberton JM, Kruuk LEB, Clutton-Brock TH. 2011 Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. *J. Evol. Biol.* **24**, 772–783. (doi:10.1111/j.1420-9101.2010.02212.x)
 75. Brommer JE, Rattiste K, Wilson AJ. 2008 Exploring plasticity in the wild: laying date–temperature reaction norms in the common gull *Larus canus*. *Proc. R. Soc. B* **275**, 687–693. (doi:10.1098/rspb.2007.095)
 76. Sih A, Waters JV. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour* **142**, 1417–1431. (doi:10.1163/156853905774539454)
 77. Both C, Dingemanse NJ, Drent PJ, Tinbergen JM. 2005 Pairs of extreme avian personality have highest reproductive success. *J. Anim. Ecol.* **74**, 667–674. (doi:10.1111/j.1365-2656.2005.00962.x)
 78. Cote J, Clobert J. 2007 Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. B* **274**, 383–390. (doi:10.1098/rspb.2006.3734)
 79. Cote J, Fogarty S, Sih A. 2012 Individual sociability and choosiness between shoal types. *Anim. Behav.* **83**, 1469–1476. (doi:10.1016/j.anbehav.2012.03.019)
 80. Saltz JB, Foley BR. 2011 Natural genetic variation in social niche construction: social effects of aggression drive disruptive sexual selection in *Drosophila melanogaster*. *Am. Nat.* **177**, 645–654. (doi:10.1086/659631)